



# A study of the biology of *Epicharis (Epicharoides) picta* using emergence-traps

Hugo de Azevedo Werneck<sup>1,2</sup>, Lucio Antonio de Oliveira Campos<sup>1</sup>

**1** Departamento de Biologia Geral, Universidade Federal de Viçosa, Avenida Ph Rolfs s/n, 36.570-000, Viçosa, MG, Brazil **2** Departamento de Entomologia, Universidade Federal de Viçosa, Avenida Ph Rolfs s/n, 36.570-000, Viçosa, MG, Brazil

Corresponding author: Hugo de Azevedo Werneck (beehugo@gmail.com)

---

Academic editor: Jack Neff | Received 26 July 2020 | Accepted 12 November 2020 | Published 29 December 2020

<http://zoobank.org/45EE4D19-FECD-4B1E-9266-D020E9DDF1A0>

---

**Citation:** Werneck HA, Campos LAO (2020) A study of the biology of *Epicharis (Epicharoides) picta* using emergence-traps. Journal of Hymenoptera Research 80: 147–167. <https://doi.org/10.3897/jhr.80.56898>

---

## Abstract

This study investigates the nesting habits of *Epicharis picta* in a nest aggregation located in a fragment of the Atlantic forest in Southeastern Brazil. Ten emergence-traps were set up in this nest aggregation to standardize data collection of phenology, natural enemies, and sex ratio. *Epicharis picta* nests were in an area of 160 m<sup>2</sup> with a density of 41 nests/m<sup>2</sup>. Nest and cell architecture are described. *Epicharis picta* is a protandrous, univoltine species with its emergence in this study occurring between 28 January and 15 April. We provide direct evidence of parasitism on *E. picta* by *Rhathymus friesei*, *Tetraonyx sexguttata* and *T. aff. lycoides*. The predator *Apiomerus lanipes* was found to prey *Epicharis* for the first time. We suggest the use of emergence-traps as tools to support studies of ground-nesting bees. In addition, we compile, update, and discuss data on the nesting biology of all *Epicharis* subgenera.

## Keywords

Cleptoparasitism, Emergence-trap, Ground-nesting bees, Nest architecture, Solitary bees

## Introduction

Solitary bees use a wide variety of nesting substrates, digging their nests in soil or wood, constructing freestanding nest, or using pre-existing cavities (Michener 1974, 2007). In fact, most of them nest in the ground (Linsley 1958; Batra 1984; Roubik 1989; Michener 2007), which may be a plesiomorphic condition among bees

(Michener 1964, 2007; Radchenko 1996). This variety of nesting habits gives rise to a wide diversity of life cycles, nest architecture, nesting behaviors, and relationships with their natural enemies.

*Centridini* is a neotropical tribe of oil-collecting bees, composed of only two well-supported monophyletic genera (Moure et al. 2012; Bossert et al. 2019) of solitary bees: *Epicharis* Klug, 1807, which dig their nests in the soil; and *Centris* Fabricius, 1804, composed mostly of some species that dig their nests in the soil or sometimes in termite nests (e.g., Rozen and Buchmann 1990; Gaglianone 2001; Aguiar and Gaglianone 2003; Rozen et al. 2011) and some that use pre-existing cavities (e.g., Costa and Gonçalves 2019). Even though nesting habits tend to be constant in some species, *Centris'* nesting behavior has some plasticity (Vinson and Frankie 1991; Martins et al. 2014).

*Epicharis* has nine subgenera (*Anepicharis* Moure, 1945, *Cyphepicharis* Moure, 1945, *Epicharana* Michener, 1954, *Epicharis* Klug, 1807, *Epicharitides* Moure, 1945, *Epicharoides* Radoszkowski, 1884, *Hoplepicharis* Moure, 1945, *Parepicharis* Moure, 1945 and *Triepicharis* Moure, 1945), with a total of 36 species described (Moure et al. 2012; Laroca and Nery 2018). However, there are available data on nesting biology for only 11 of them. Most species studied dig their nests exclusively in sandy soils (Roubik and Michener 1980; Raw 1992; Hiller and Wittmann 1994; Gaglianone 2005; Rocha-Filho et al. 2008; Rozen 2016; Dec and Vivallo 2019; Martins et al. 2019; Vivallo 2020a), except for *E. (Epicharana) rustica* (Olivier, 1789) (Michener and Lange 1958), *E. (Epicharana) flava* Friese, 1900 (Camargo et al. 1975), *E. (Hoplepicharis) fasciata* Lepeletier & Serville, 1828 (Vesey-FitzGerald 1939; Rozen 1965; Vivallo 2020b), *E. (Epicharitides) obscura* Friese, 1899 (Laroca et al. 1993), and *E. (Parepicharis) metatarsalis* Friese, 1899 (Thiele and Inouye 2007).

Univoltinism is the phenological pattern observed for most species of *Epicharis* (Roubik and Michener 1980; Raw 1992; Hiller and Wittmann 1994; Gaglianone 2005; Gaglianone et al. 2015; Vivallo 2020a, b), except multivoltinism for *E. flava* (Camargo et al. 1975) and bivoltinism for *E. (Epicharis) bicolor* Smith, 1854 (Rocha-Filho et al. 2008). Adult short-term activity may be a strategy that minimizes exposure to attacks by parasitic species (Wcislo 1987).

The compilation made by Gaglianone (2005) on the data known for *Epicharis'* nesting biology, does not point to any clear patterns among its nine subgenera. Hence there is a need for an increase in the quantity of species studied, particularly with regard to number of generations per year, presence or absence of diapause in the immature stages, type of soil used as substrate, depth of brood cells, number of cells per nest, plus other biological data that may aid us comparisons within and between subgenera of *Epicharis*. In addition, a phylogenetic approach of these characters compared to phylogenetic studies on *Centridini* (e.g., Martins and Melo 2016) can elucidate evolutionary aspects of these bees.

The natural enemies of *Epicharis*, include parasitoids, cleptoparasitic, and predatory insects. Bees of the genus *Rhathymus* (Apidae, Rhathymini) are known to be specialized cleptoparasites of *Epicharis'* nests (compiled by Werneck et al. 2012),

although there are also more generalized cleptoparasites, such as those of the genus *Mesoplia* Lepeletier, 1841 (Apidae, Ericrocidini) which also attack nests of *Centris* (Gaglianone 2005; Rocha-Filho et al. 2008; Rocha-Filho et al. 2009; Vivallo 2020a). Besides bees, there are records of *Epicharis* as a host for both cleptoparasitic species of Meloidae (Coleoptera) and parasitoid species of Conopidae (Diptera) and Mutillidae (Hymenoptera) (Gaglianone 2005; Rocha-Filho et al. 2008; Gaglianone et al. 2015). Despite the scarcity of information in the literature, species of Hemiptera, especially those of the genus *Apiomerus* (Reduviidae), are known to be predators of adult bees (Silva and Amaral 1973; Cane 1986; Amaral-Filho et al. 1994; Marques et al. 2003, 2006; Silva and Gil-Santana 2004).

Studies on the nesting biology, relationships with natural enemies, and phenology of *Epicharis* species have been performed using direct observations of nest aggregations. Nonetheless, there is a need for methods that provide standardization for data collection. To this aim, emergence-traps have been used in ground-nesting solitary bees and wasps studies and have shown to be effective in answering key questions on the biology of these insects (Hiller and Wittmann 1994; Sardiña and Kremen 2014; Rocha-Filho and Melo 2017; Cope et al. 2019).

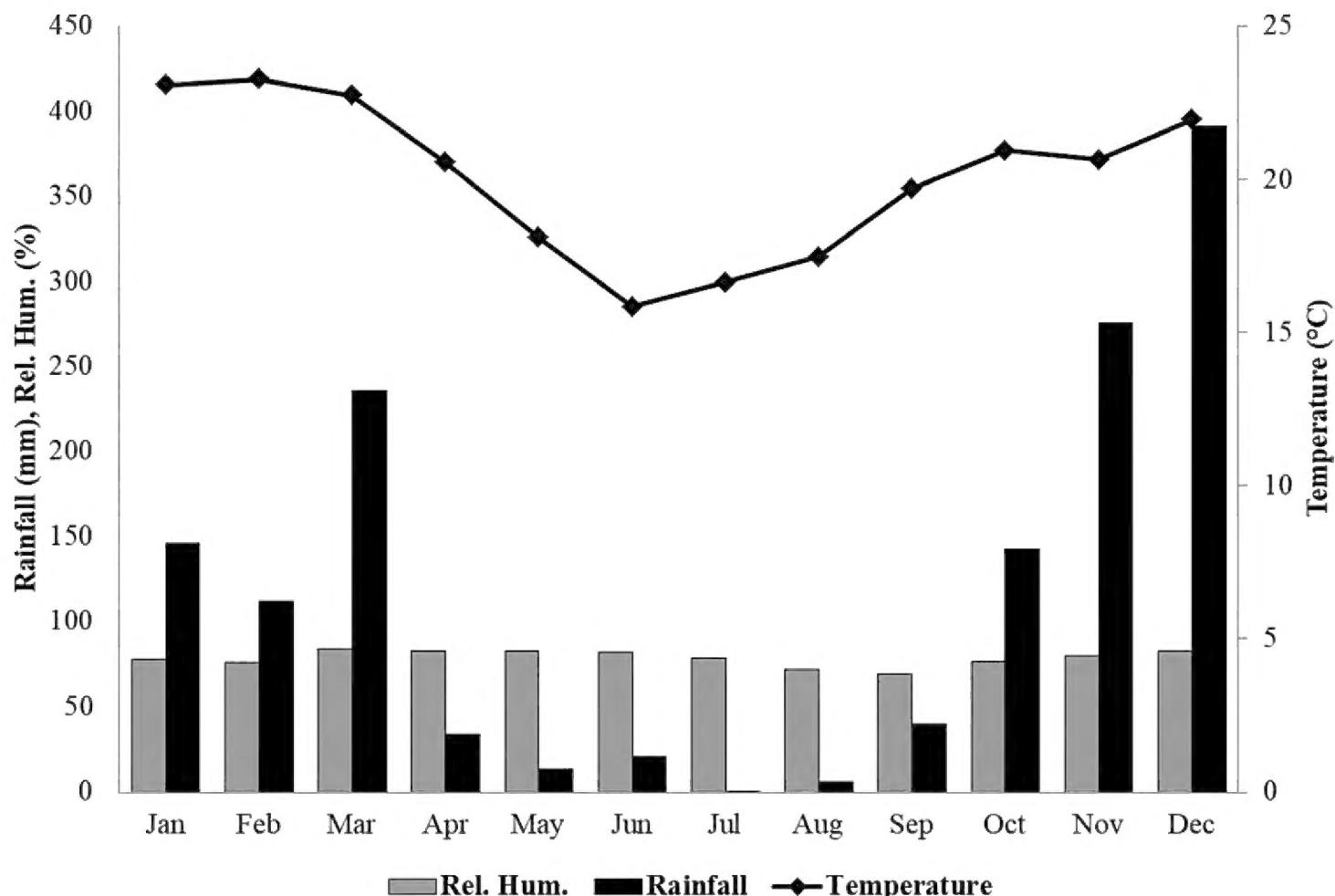
*Epicharis picta* occurs in Uruguay, Paraguay, Argentina, and Brazil (Federal District and the states of Espírito Santo, Minas Gerais, Paraná, Paraíba, Rio de Janeiro, Santa Catarina, and São Paulo – Moure et al. 2012). Its life cycle is univoltine (Gaglianone et al. 2015) and it is oligolectic on Malpighiaceae (Werneck et al. 2015). However, data on its nesting behavior, nests and cell architecture, and natural enemies are scarce in the literature.

In this study, we investigated the nesting habits of *Epicharis picta* for two years and provide information on its biology, natural enemies, nest and cell architecture, sex ratio, and phenology, based on direct observations and emergence-traps data. An updated compilation of nesting biology and nest architecture data of the *Epicharis* genus is also provided.

## Material and methods

### Study site

The nest aggregation of *Epicharis picta* studied was in a fragment of semideciduous, montane and submontane Atlantic Forest (Veloso et al. 1991), in the municipality of Viçosa, Minas Gerais-Brazil, on the access road to the Estação de Pesquisa, Treinamento e Educação Ambiental Mata do Paraíso ( $20^{\circ}47'56"S$ ,  $42^{\circ}52'07"W$ ) (see Gaglianone et al. 2015). The climate of the region is temperate, rainy (mesothermal), with hot and rainy summers, and cool and dry winters (type Cw, according to the classification of Köppen – Köttek et al. 2006). The climatological data of the region between 2009 and 2011 are shown in Fig. 1.



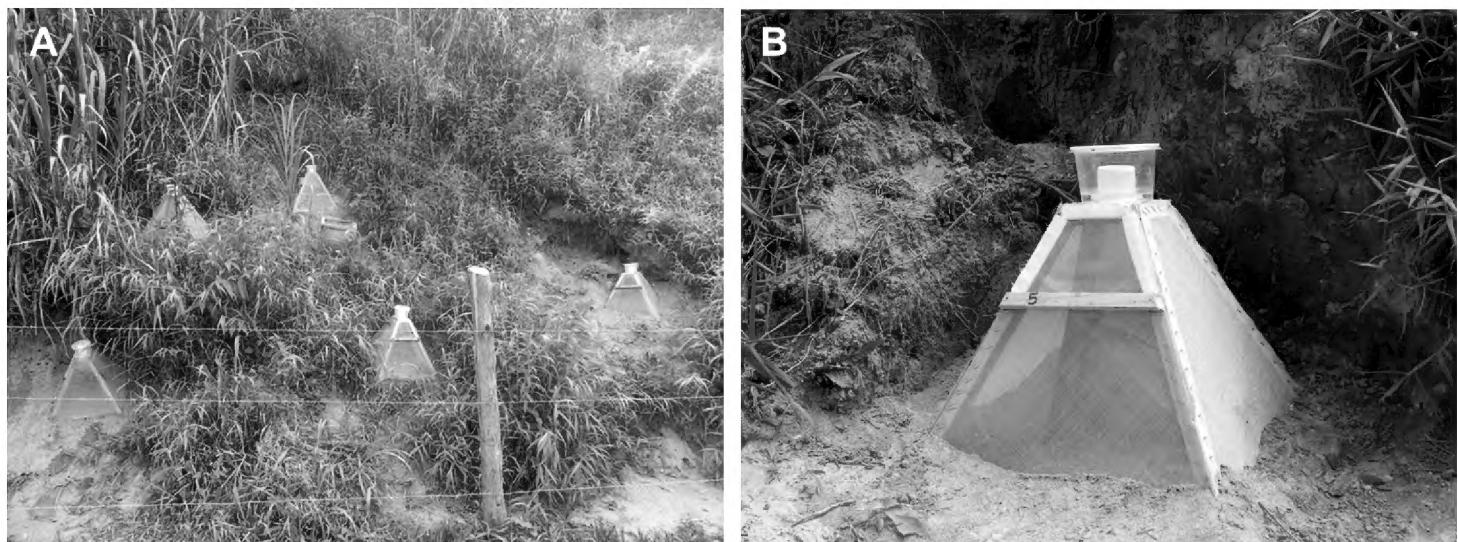
**Figure 1.** Climatological data from Viçosa, Minas Gerais-Brazil, between 2009 and 2011 (Source: Estação Climatológica Principal de Viçosa, Departamento de Engenharia Agrícola – UFV).

### Nesting biology, nest architecture, and brood cells

The fieldwork was carried out for two years. In 2010, visits took place monthly; and in 2011, daily, during the period of activity of the adult bees. The nesting habits of *E. picta* were obtained from direct observations throughout each day from 5:30 h to 19:00 h. To study the brood cells, eight excavations were made in 50 cm × 50 cm plots. The brood cells found in the soil were collected, placed in plastic pots with substrate from the nesting site, and kept in the laboratory to assess their content and dimensions. For nest architecture, as the main burrow remains open after a nest is completed, we injected plaster in five nests. Ten plots of 1 m<sup>2</sup> were randomly set up in the aggregation to estimate nest density.

### Emergence-traps, natural enemies, and associated species

To standardize the sampling method when studying phenology, sex ratio, and parasite-host synchrony, 10 emergence-traps were randomly set up at the nesting site from 20 January to 20 May 2011 (Fig. 2A). The emergence-traps consisted of a pyramid-shaped wooden frame covered with thin nylon mesh, with the following dimensions: 50 cm × 50 cm base, 10 cm × 10 cm top end, and 50 cm height (Fig. 2B). On one side, a 12 cm long opening was made in the longitudinal direction to install a Velcro



**Figure 2.** Emergence-traps set up on aggregate of *Epicharis (Epicharoides) picta* (**A**); Detail of emergence-trap (**B**).

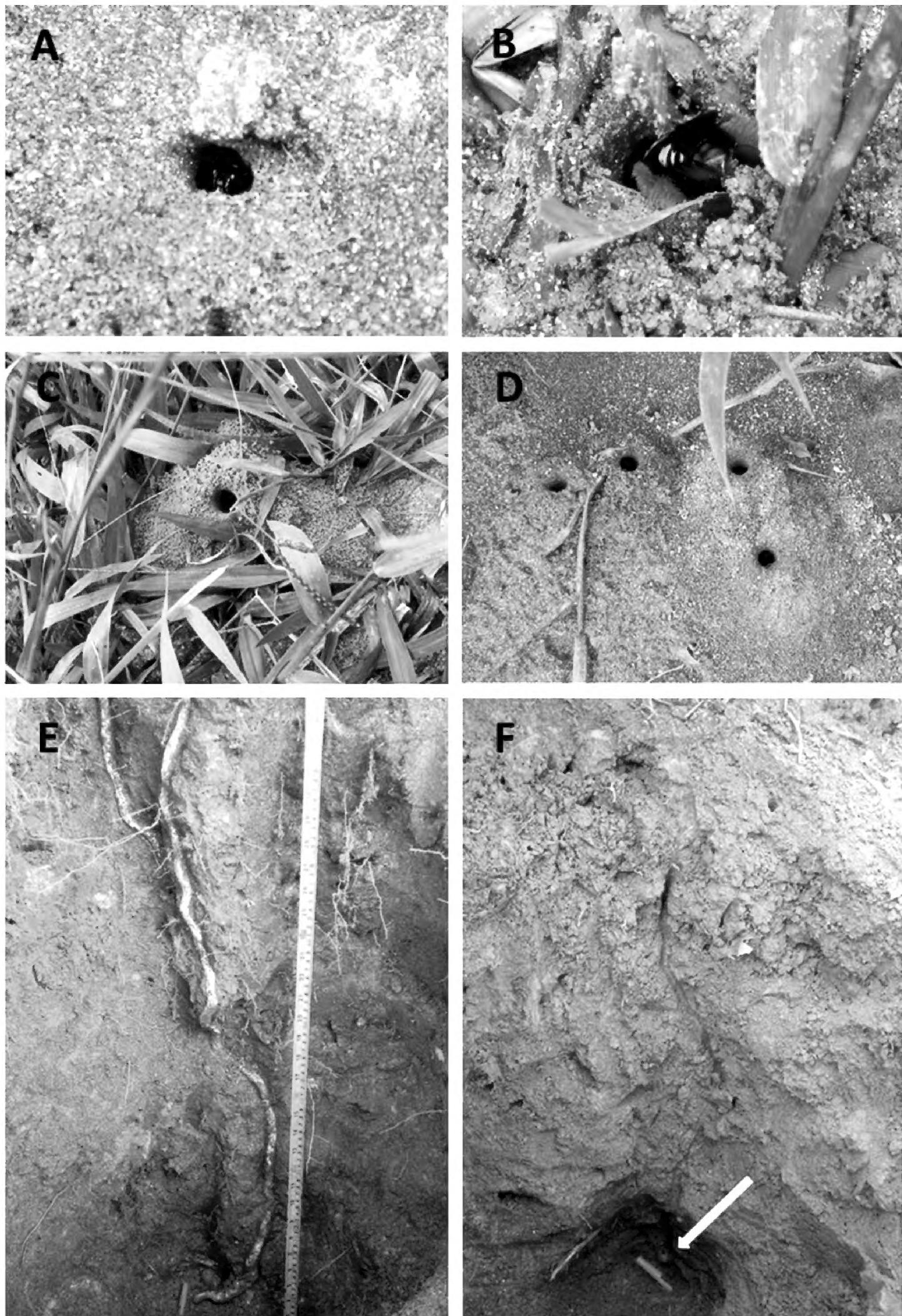
tape, forming a “window” that allowed our access to its interior. (Fig. 2B). A piece of PVC pipe attached to a plastic container was placed at the upper end with its bottom facing the interior of the trap and its top inside the plastic container, which was filled with a 1:1 alcohol and water solution (Fig. 2B). Inspections on emergence-traps were conducted daily.

Data on potential natural enemies and associated species that were seen visiting the nest aggregation area were collected throughout the study period. Vouchers from the specimens studied are deposited at Museu Regional de Entomologia, Departamento de Entomologia-Universidade Federal de Viçosa (MEUFV). This study follows the classification system of Moure et al. (2007), which treats the whole group of bees as a single family (Apidae).

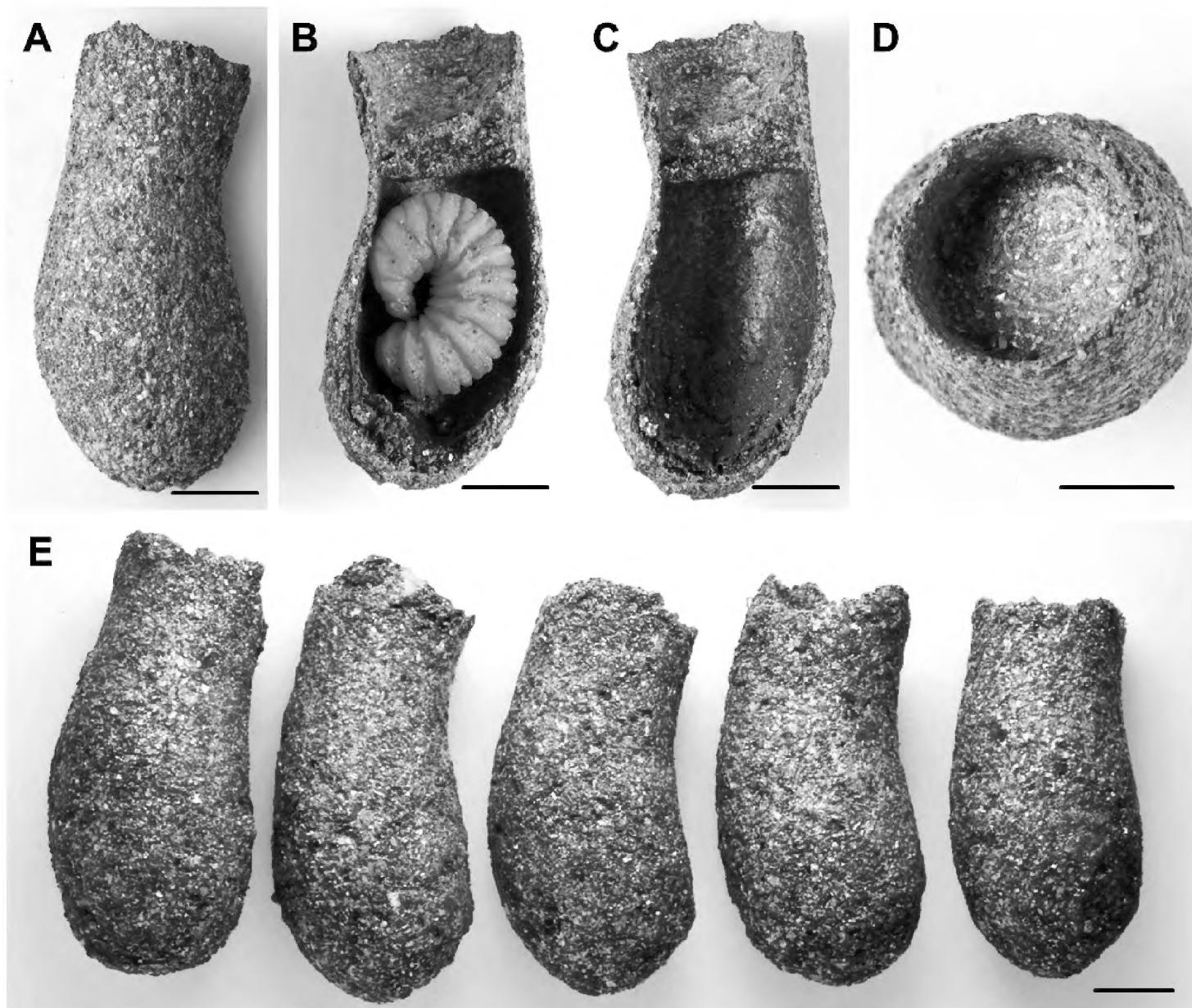
## Results

### Nesting biology, nest architecture, and brood cells

*Epicharis picta* nests were aggregated in an area of approximately 160 m<sup>2</sup> of exposed slopes of about 45°, with an average nesting density of 41 entrances/m<sup>2</sup>. Females began their activities between 6:00 h and 6:30 h and ended between 18:00 h and 18:30 h, daily. The activity peak occurred between 7:30 h and 11:30 h. The females rested inside the nests at night (Fig. 3A). Male activity period was shorter, between 6:00 h and 16:00 h. The mating male behavior is being dealt in a separate study. Every day at the beginning of activities (~6:00 h), females took about five minutes at the nest entrance before making their first flight. After their first trip, their scopae were still clean when they returned, with no evidence of oil or pollen having been collected (Fig. 3B). For digging new nests, they selected a new nest site, excavated the soil vertically, using their mandibles, anterior and middle legs, and deposited the material from the excavation around the nest entrance, forming a circular tumulus (Fig. 3C, D).



**Figure 3.** Nesting habits and nest architecture of *Epicharis (Epicharoides) picta* **A** female resting inside the nests at night **B** female of *E. picta* excavating nest **C, D** entrance of the nests showing the presence of a tumulus **E, F** architecture of 110 cm deep nests.



**Figure 4.** Brood cells of *Epicharis (Epicharoides) picta* **A** outer cell wall surface **B** mature larva inside the cell **C** inner cell wall surface **D** the cell cap inserted below the apex of the cell wall **E** variation in brood cell shape. Scale bars: 5 mm.

The excavated nests ( $N = 8$ ) contained one to two cells each. In nests with only one cell ( $N = 6$ ), there was a single tunnel (Fig. 3E, F), whereas in nests containing two cells at the end of the main tunnel ( $N = 2$ ), a branch with no cell was also found. The diameter of these tunnels ranged from 10 mm to 12 mm ( $N = 20$ ). The nests were perpendicular to the surface, ranging from 50 cm to 110 cm deep.

The brood cells were slightly curved (Fig. 4A–E) and built at an angle of about 45° to the ground surface. Their outer walls are rough and rigid, whereas inner walls are smooth, shiny, and hydrophobic (Fig. 4A–C). The cell cap is inserted below the apex of the cell wall and is slightly inclined (Fig. 4D). The cells size ranged from 20 mm to 27 mm ( $\bar{X} = 24.57$  mm;  $N = 27$ ) in length, between 10 mm and 12 mm ( $\bar{X} = 11.12$  mm;  $N = 27$ ) in diameter at cell cap height, and the base diameter between 12 mm and 14.5 mm ( $\bar{X} = 13.74$  mm;  $N = 27$ ).

Females of *Epicharis (Epicharoides) albofasciata* were observed founding nests ( $N = 14$ ) in the aggregation of *E. picta*. Only one nest of *E. albofasciata* was excavated, and it consisted of a single 35 cm deep tunnel with one cell at its end. Agonistic

behavior among females of *E. picta* and *E. albofasciata* was observed when females returned from the field. *E. albofasciata* males were neither observed nor collected on the nest aggregation during fieldwork.

### **Emergence-traps, phenology, and sex ratio**

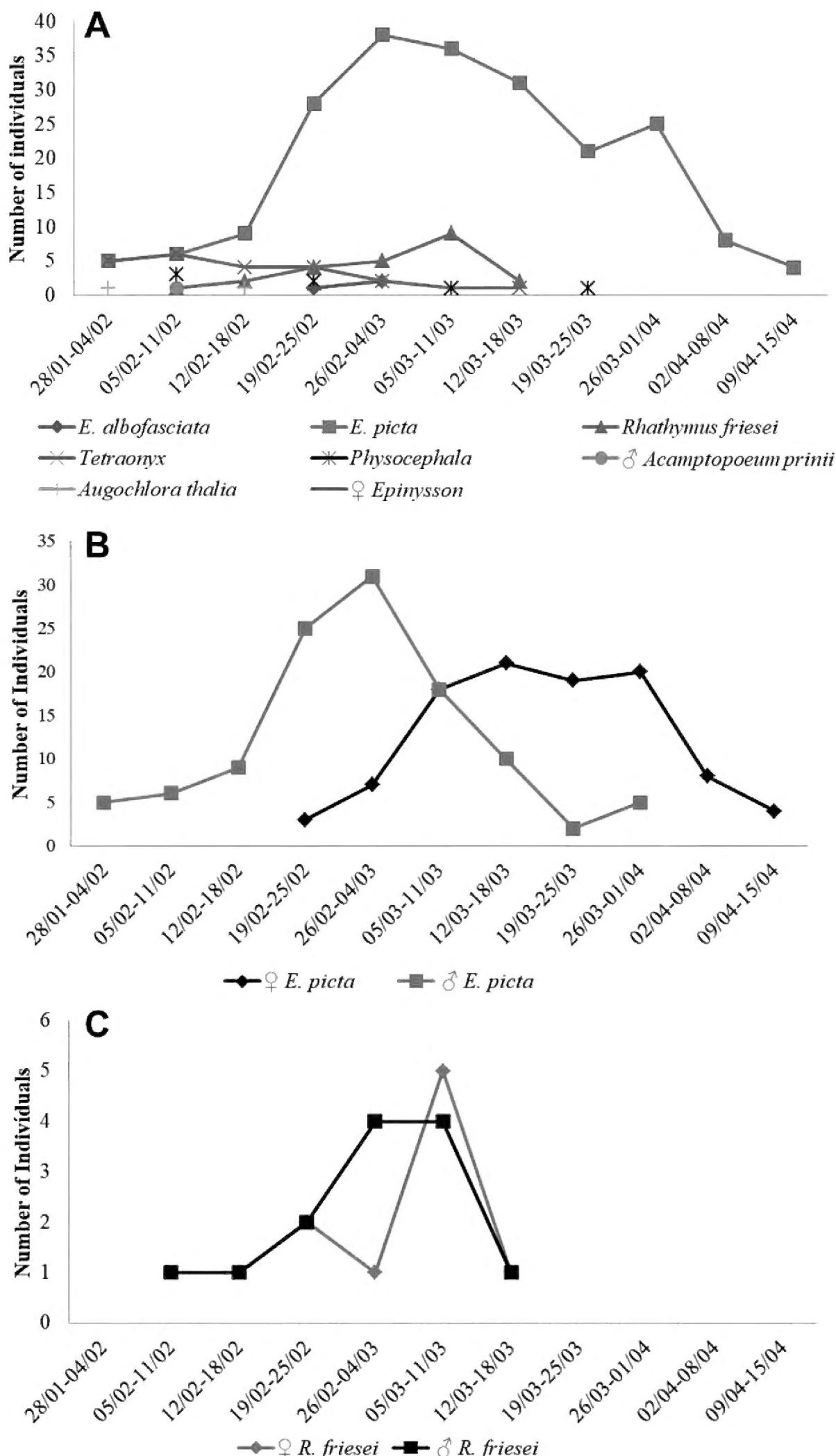
Ten emergence-traps were set in the aggregation for 121 days, between 20 January and 20 May 2011. The emergence period in the traps was from 28 January to 15 April 2011. The emergence peak, encompassing all species, occurred from 19 February to 18 March (Fig. 5A). From the 271 individuals that emerged in the emergence-traps, *E. picta* was the most abundant species (211, 78%), followed by *Rhathymus friesei* (23, 8.5%), *Tetraonyx sexguttata* (Meloidae) (18, 6.65%), *Phyocephala* sp. (Conopidae) (7, 2.55%), *Tetraonyx* aff. *lycoides* (5, 1.85%), *E. albofasciata* (3, 1.10%), *Augochlora thalia* (Apidae, Augochlorini) (2, 0.71%), *Acamptopoeum prinii* (Apidae, Calliopsini) (1, 0.32%), and *Epinysson* sp. (Crabronidae, Nyssonini) (1, 0.32%).

*Epicharis picta* first appeared in the emergence-traps on 29 January, and males were the first to emerge (Fig. 5B), indicating protandry. From a total of 211 individuals, 111 were male (52.6%), and 100 female (47.4%). Thus, the sex ratio of *E. picta* was 1.11 males to 1 female. *Rhathymus friesei* emerged from 5 February to 18 March, peaking from 26 February to 11 March. Males were the first to emerge, on 5 February, whereas females emerged from 19 February, which also indicates protandry (Fig. 5C). From the 23 emerged individuals, 13 were males (56.53%) and 10 were females (43.47%), resulting in a sex ratio of 1.3 males to 1 female.

### **Natural enemies and associated species sampled from direct observations**

In addition to species sampled from the emergence-traps, we collected another 24 species of insects found in the area, which were then identified and classified according to their association with the nesting aggregation (Table 1). *Rhathymus friesei* was the most abundant natural enemy (Fig. 6A); in some moments, up to four individuals could be seen inspecting the nest aggregation at the same time. *Tetraonyx sexguttata* was observed walking on the aggregation, landing on vegetation, and emerging from *E. picta* nests (Fig. 6B). Individuals of *Apiomerus lanipes* were observed five times near the entrances of the nests capturing females of *E. picta* when those entered or left their nest. The predator attacked the prey with its forelegs, inserting the stylet between the thorax and the head (Fig. 6C). Twenty-seven individuals of Mutillidae were collected in the aggregation. However, only one female of *Traumatomutilla* sp. was observed directly inspecting *E. picta* nests (Fig. 6D). *Phyocephala* sp. specimens were also observed flying over the nest site between 5 February and 22 March.

Females of *Augochloropsis* cf. *cupreola* (Apidae, Augochlorini), *Hypanthidium nigritulum* (Apidae, Anthidiini), and *Colletes petropolitanus*, (Apidae, Colletini) were observed performing inspection flights over the soil and branches of vegetation in the aggregation, but they neither nested nor interacted with *E. picta* females. *Trigona spinipes*



**Figure 5.** Emergence patterns in the emergence-traps set up on the nest aggregation of *Epicharis (Epicharoides) picta* **A** emergence of all species sampled in the traps **B** emergence of the males and females of *E. picta* **C** emergence of the males and females of *Rhathymus friesei*.

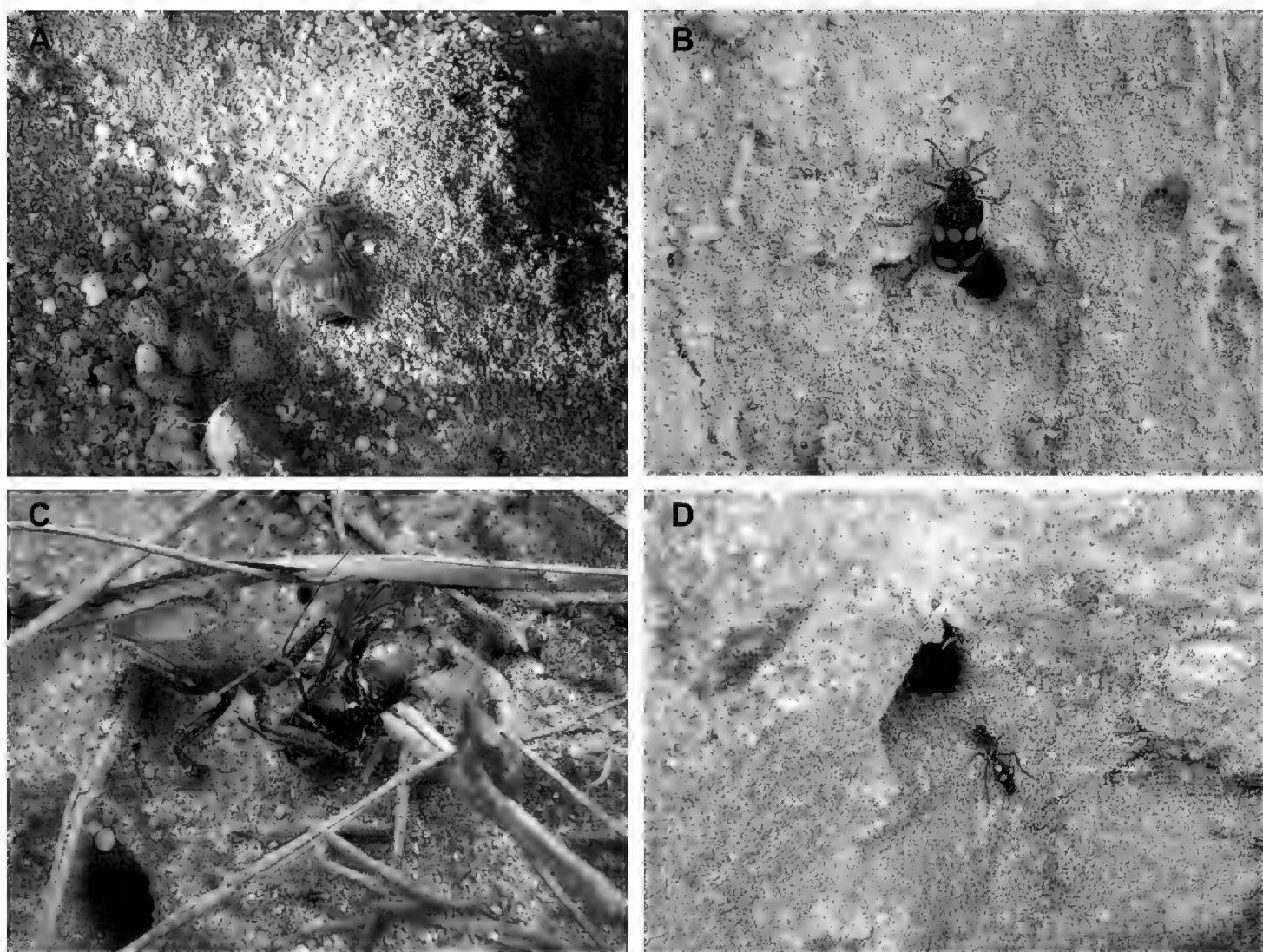
**Table I.** Natural enemies and associated species from a nesting aggregation of *Epicharis* (*Epicharoides*) *picta*. Type of evidence for potential parasitoids, cleptoparasites or predators: \*Indirect evidence; \*\*Direct evidence.

Order	Family	Tribe	Species	Type of association
Diptera	Conopidae	Physocephalini	<i>Physocephala</i> sp.	Parasitoid*
Coleoptera	Meloidae	Tetraonycini	<i>Tetraonyx</i> ( <i>Tetraonyx</i> ) <i>sexguttata</i> (Olivier, 1795)	Cleptoparasite**
			<i>Tetraonyx</i> aff. <i>lycooides</i>	Cleptoparasite**
Hemiptera	Reduviidae	Apiomerini	<i>Apiomerus lanipes</i> (Fabricius, 1803)	Predator**
Hymenoptera	Apidae	Anthidiini	<i>Hypanthidium nigritulum</i> Urban, 1998	No direct association
		Augochlorini	<i>Augochlora thalia</i> Smith, 1879	No direct association
			<i>Augochloropsis</i> cf. <i>cupreola</i> (Cockerell, 1900)	No direct association
		Calliopsini	<i>Acamptopoeum prinii</i> (Holmberg, 1884)	No direct association
		Centridini	<i>Epicharis</i> ( <i>Epicharoides</i> ) <i>albofasciata</i> Smith, 1874	No direct association
		Colletini	<i>Colletes petropolitanus</i> Dalla Torre, 1896	No direct association
		Ericocidini	<i>Mesoplia rufipes</i> (Perty, 1833)	Cleptoparasite*
		Meliponini	<i>Trigona spinipes</i> (Fabricius, 1793)	No direct association
		Rhathymini	<i>Rhathymus friesei</i> Ducke, 1907	Cleptoparasite**
	Crabronidae	Larrini	<i>Tachysphex</i> sp. 1	No direct association
			<i>Tachysphex</i> sp. 2	No direct association
			<i>Tachysphex</i> sp. 3	No direct association
		Nyssonini	<i>Epinysson</i> sp.	No direct association
	Mutillidae	Ephutini	<i>Ephuta</i> sp. 1	Parasitoid*
			<i>Ephuta</i> sp. 2	Parasitoid*
		Sphaeropthalmini	<i>Hoplocrates cephalotes</i> (Swederus, 1787)	Parasitoid*
			<i>Hoplomutilla spinosa</i> (Swederus, 1784)	Parasitoid*
			<i>Pseudomethoca macropis</i> (Gerstaecker, 1874)	Parasitoid*
			<i>Pseudomethoca</i> sp. 1	Parasitoid*
			<i>Pseudomethoca</i> sp. 2	Parasitoid*
			<i>Pseudomethoca</i> sp. 3	Parasitoid*
			<i>Traumatomutilla inermis</i> (Klug, 1821)	Parasitoid*
			<i>Traumatomutilla</i> sp.	Parasitoid*
			<i>Traumatomutilla trochantera</i> (Gerstaecker, 1874)	Parasitoid*
Sphecidae	Ammophilini		<i>Ammophila</i> sp.	No direct association
	Sphecini		<i>Sphex</i> sp.	No direct association
Vespidae	Eumenini		<i>Pirhosigma superficiale</i> (Fox, 1899)	No direct association

(Apidae, Meliponini) workers landed on the nest site and collected soil material removed by *E. picta* females during the excavation of their nests. A female of *Mesoplia rufipes* was collected on 20 March 2010. This bee flew over the aggregation and periodically approached some entrances of *E. picta* nests. However, it was not seen entering any nest.

### Brood cells collected during excavations

In the two years of studies, a total of 121 cells were collected, ranging between 30 cm and 110 cm deep. From these, 45 were already open, containing only soil in their interior. Six cells were taken by fungi, one of which contained a dead *E. picta* female pupae (Fig. 7A). Another six cells containing only fungi on the food (Fig. 7B) with no evidence of dead larvae or egg, nor parasitic traces. In one cell there was an exoskeleton of *T. sexguttata* (Fig. 7C). In the 46 cells, there were 38 mature larvae (Fig. 4B) and eight pupae of *E. picta*. From the 17 cells kept in the laboratory throughout



**Figure 6.** Natural enemies and associated species of *Epicharis (Epicharoides) picta* **A** *Rhathymus friesei* inspecting at the nest aggregation **B** *Tetraonyx sexguttata* emerging from a nest of *E. picta* **C** *Apiomerus lanipes* preying on a female of *E. picta* **D** *Traumatomutilla* sp. inspecting the entrance of a nest of *E. picta*.

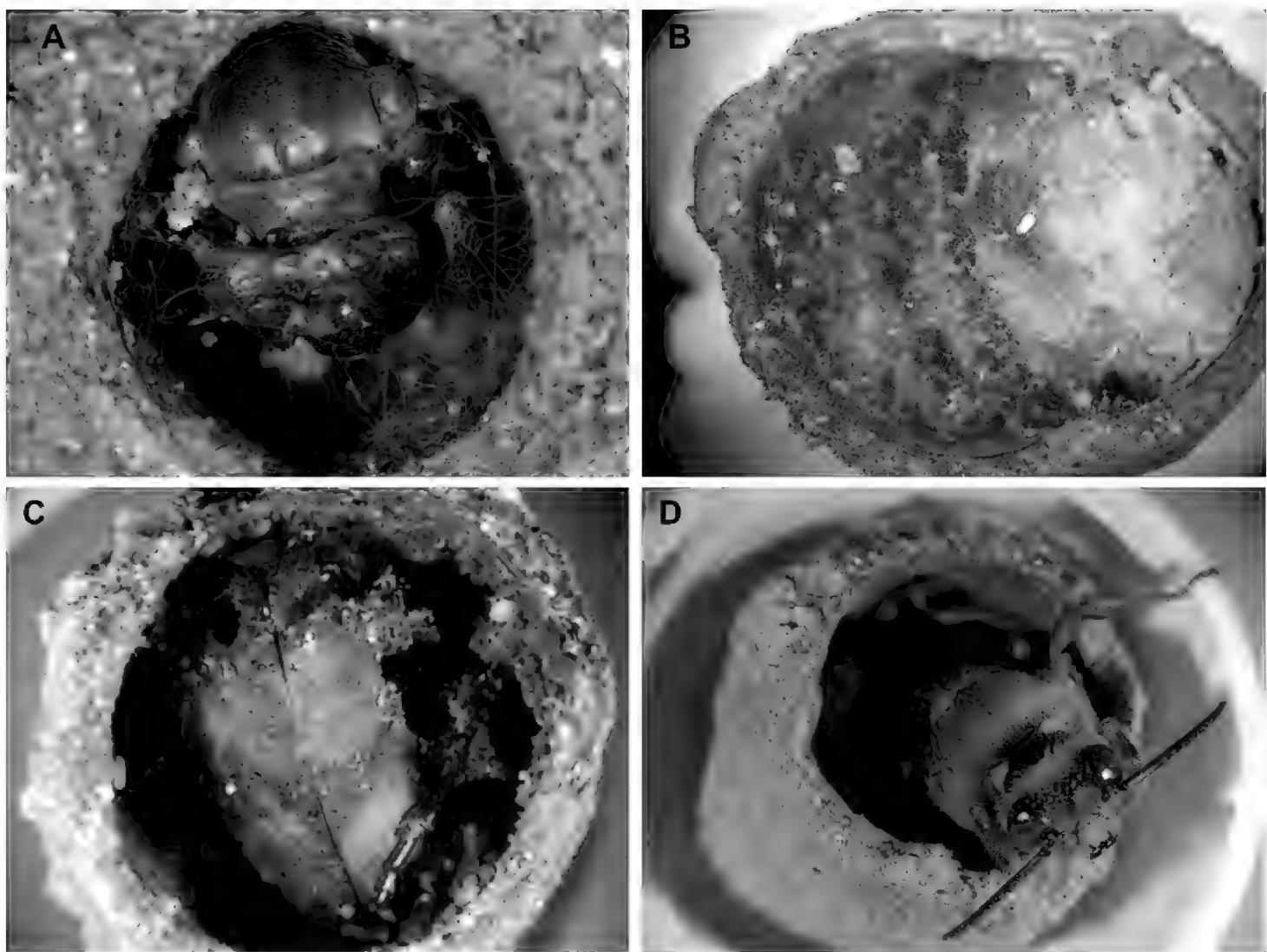
the year, four males (Fig. 7D) and six females of *E. picta*, two *T. sexguttata*, and one *T. aff. lycoides* emerged. In the remaining four cells, there were mature larvae of *R. friesei*. Larvae of *R. friesei* were easy to identify due to the presence of their cocoon (see Rozen 1969; Camargo et al. 1975; Werneck et al. 2012).

## Discussion

Studies reporting biological data about *E. picta* are recent in the literature (Werneck et al. 2012; Werneck et al. 2015; Gaglione et al. 2015). These, however, do not address aspects related to their nesting habits, natural enemies, and associated species. Therefore, this present study is the first to bring such data, in addition to using emergence-traps as a model.

### Nesting biology and notes on patterns among *Epicharis* subgenera

Our data on *E. picta* reinforce the hypothesis that all species of *Epicharis* nest gregariously in the soil (Vesey-FitzGerald 1939; Michener and Lange 1958; Rozen 1965;



**Figure 7.** Content of *Epicharis (Epicharoides) picta* brood cells **A** dead *E. picta* female pupa with fungus **B** food in *E. picta* brood cell taken by fungus **C** exoskeleton of *Tetraonyx sexguttata* **D** male of *E. picta* emerged from brood cell maintained in laboratory.

Camargo et al. 1975; Roubik and Michener 1980; Raw 1992; Laroca et al. 1993; Hiller and Wittmann 1994; Gaglianone 2005; Thiele and Inouye 2007; Rocha-Filho et al. 2008; Rozen 2016; Dec and Vivallo 2019; Martins et al. 2019; Vivallo 2020a, b). In spite of the low quantity of species studied, it is possible to point to a pattern on the exclusive use of sandy soil for nesting by the subgenera *Epicharoides*, *Epicharis*, *Triepicharis* and *Anepicharis* (Table 2). Although *Parepicharis* also uses sandy soil, there are records of *E. metatarsalis* nesting in clay (Thiele and Inouye 2007). For *Epicharana*, there seems to be some preference over nesting in low light places, as recorded for *E. flava* (Camargo et al. 1975), *E. rustica*, and *E. elegans* (Michener and Lange 1958). Despite that, it is not possible to point to any patterns regarding nest depth, which can vary according to the characteristics of each site used for nesting (Cane 1991), nest density, and the number of brood cells per nest. A study of phylogenetic reconstruction based on nesting behavior characters encompassing the whole Centridini tribe is under way (Werneck HA, unpublished data). As a result, we expect a better understanding of the patterns and evolution of these characteristics. For a comparison of the characteristics regarding nesting habits amongst the species of *Epicharis* studied, see Table 2.

**Table 2.** Compilation of comparative data on nesting biology of the genus *Epicharis*.

	<i>E. (Epicharoides) picta<sup>a</sup></i>	<i>E. (Epicharoides) albofasciata<sup>a,b,c</sup></i>	<i>E. (Epicharis) bicolor<sup>d</sup></i>	<i>E. (Epicharis) nigrita<sup>e</sup></i>	<i>E. (Parepicharis) metatarsalis<sup>f</sup></i>	<i>E. (Parepicharis) zonata<sup>g</sup></i>	<i>E. (Triepicharis) analis<sup>h</sup></i>	<i>E. (Anepicharis) dejeanii<sup>i,j,k,l,**</sup></i>	<i>E. (Triepicharis) analis<sup>**</sup></i>	<i>E. (Epicharides) dejeanii<sup>j</sup></i>	<i>E. (Hoplepicharis) fasciata<sup>o</sup></i>	<i>E. (Epicharides) obscur<sup>n</sup></i>
Phenology	univoltine	univoltine	bivoltine	univoltine	univoltine	univoltine	univoltine	multivoltine	univoltine	multivoltine	univoltine	?
Nesting place	slanted	slanted	flat	flat	flat	flat	flat	vertical	vertical/flat	flat	wet soil	?
Soil type	sandy soil	sandy soil	sandy soil	sandy soil	clay and sandy soil	sandy soil, seasonally swamp	sandy soil	sandy soil	basalt afforation	earth bank/sandy soil	wet soil	
Nest arrangement	aggregated	aggregated	aggregated	aggregated	aggregated	aggregated	aggregated	aggregated	aggregated	aggregated	aggregated	?
Nest type	one tunnel, branched	one tunnel	one tunnel	one tunnel branched	one tunnel, branched	one tunnel, branched	one tunnel, branched	one tunnel, branched	one tunnel, branched	one tunnel, branched	one tunnel	one tunnel
Nest density	41/m <sup>2</sup>	1/m <sup>2</sup>	40/m <sup>2</sup>	3–32/m <sup>2</sup>	25/m <sup>2</sup>	12/m <sup>2</sup>	0.31/m <sup>2</sup>	1–25/m <sup>2</sup>	?	1.5/m <sup>2</sup>	?	?
Cell arrangement	isolated, end of tunnels	isolated, end of tunnels	linear	isolated, end of tunnels	isolated, end of tunnels	isolated, end of tunnels	isolated, end of tunnels	isolated, end of tunnels	linear	isolated, end of tunnels	isolated, end of tunnels	
Cell position	slanted	slanted	transversal, horizontal or vertical	slanted	vertical	vertical	slanted, horizontal	horizontal	vertical	vertical	vertical	
Cell per nest	1–2	1–6	1–2	1–5	1	1–7	2–5	1–10	1–3	1–2	1	
Cell length	20–27 mm	15–23 mm	21 mm	20–25 mm	?	24–30 mm	30 mm	29–36 mm	23–25 mm	28 mm	16.7 mm	
Cell diameter	10–14.5 mm	9.5–11.5 mm	14.5 mm	20–25 mm	?	14–20 mm	13–18 mm	19–20 mm	13–15 mm	13–15 mm	12.5 mm	
Cell depth	30–110 cm	16–35 cm	10–25 cm	16–60 cm	62–120 cm	15–52 cm	30–45 cm	25–140 cm	110 cm	30 cm	10–30 cm	

<sup>a</sup>Table adapted and updated from Gaglianone (2005);<sup>b</sup>This study; <sup>c</sup>Gaglianone (2005); <sup>d</sup>Rozén (2016); <sup>e</sup>Rocha-Filho et al. (2008); <sup>f</sup>Martins et al. (2019); <sup>g</sup>Thiele and Inouye (2007); <sup>h</sup>Raw (1992); <sup>i</sup>Hiller and Wittmann (1994); <sup>j</sup>Dec and Vivallo (2019); <sup>k</sup>Camargo et al. (1975); <sup>l</sup>Visey-FitzGerald (1939); <sup>m</sup>Laroca et al. (1993); <sup>n</sup>Vivallo (2020a); <sup>o</sup>Vivallo (2020b)<sup>\*\*</sup>The data on *E. (Triepicharis) analis* were joined with those on *E. (Triepicharis) schrottkyi*, described by Gaglianone (2005), due to the proposal of *E. schrottkyi* as a junior synonym for *E. analis* by Vélez and Silveira (2006).<sup>\*\*</sup>Cited by Raw (1992) as *E. (Anepicharis) melanoxantha*. Werneck et al. (2012) reported that *E. melanoxantha* corresponds to *E. dejeanii*. Here, we joined the data from Raw (1992) with the available data for *E. dejeanii*;

Species that nest in the soil in aggregations might also build their nests in the nest aggregations of other species (Michener 1974). For instance, there are reports of *E. albofasciata* building their nests in *E. nigrita* (Gaglianone 2005) and *E. picta* (this study) nest aggregations. However, these bees can build their own nest aggregation, as described by Rozen (2016). The characteristics described by Rozen (2016), such as nest depth, presence of a tumulus around the entrance of each nest, female preference for inclined sites (about 45°), and shape and composition of the brood cells, corroborate the findings and allow us to point out that these characteristics may be diverse within *Epicharoides*.

The development of immature stages seems to be more constant within *Epicharis*. Both *E. picta* and *E. albofasciata* present the same hatching pattern, with the presence of a pharate first instar, which is also recorded for *E. flava* and *E. nigrita* (Camargo et al. 1975; Gaglianone et al. 2015). Pharate first instar larvae were also observed for *Centris flavofasciata* Friese, 1899 (Rozen et al. 2011), in addition to other groups of solitary bees that nest in the soil, such as *Monoeca haemorrhoidalis* (Smith, 1854) (Apidae: Tapinotaspidini) (Rozen et al. 2006).

## **Emergence-traps and phenology**

Emergence-traps have been effective in collecting data on species of bees and wasps nesting in the soil (Hiller and Wittmann 1994; Sardiña and Kremen 2014; Rocha-Filho and Melo 2017; Cope et al. 2019; Martins et al. 2019). In the present study, these emergence-traps were useful for sampling data on natural enemies that emerged in the nest aggregation as well as in measuring the phenology and sex ratio of *E. picta*. We were able to measure the emergence patterns of both the host and its natural enemies.

Our data from emergence-traps corroborate the hypothesis that most *Epicharis* species are univoltine (see Gaglianone et al. 2015). The beginning of the emergence of *E. picta* occurred during the period of high temperatures and rainy season. The adults remained active until the middle of April, when the temperatures decreased and the rainfall declined drastically (see Fig. 1). These abiotic factors combined with other biotic features may influence in the diapause of *Epicharis*. A discussion about the biotic and abiotic factors that can influence the diapause process, and, consequently, the phenology of *Epicharis* species, can be seen in Gaglianone et al. (2015).

The emergence of *Rhathymus friesei* occurred about one week after the beginning of the *E. picta* adult activity. As cleptoparasitic species require provisioned brood cells from their hosts to oviposit (Wcislo 1987; Rozen 2001; Michener 2007), this emergence pattern was expected. Another fact that reinforces this pattern is that *Rhathymus* females lay their eggs in cells closed by the host female (Camargo et al. 1975; Rozen 1991). The strategy of parasitizing cells closed by the host is a plesiomorphic feature among the cleptoparasitic species that might have evolved from nest-building species, which could have five independent origins within bees (Litman et al. 2013).

*Tetraonyx* species reported in this study emerged in the same period of *E. picta*. These claptoparasites, unlike *Rhathymus*, are not considered specialists of *Epicharis* species. *Tetraonyx* spp. parasitize bees that nest in the soil (Roubik 1989; Gaglianone

2005; Rocha-Filho et al. 2008; Rocha-Filho and Melo 2011; Gaglianone et al. 2015), in addition to other bees that nest in trap-nests (Morato et al. 1999; Parizotto 2019).

*Augochlora thalia* and *Acamptopoeum prinii*, and *Epinysson* sp. were collected in emergence-traps. These species nest in the soil and presumably were just opportunistically using the *Epicharis* nest site. The issue of nesting in nest aggregations of other species may be related to the strategy of inhibiting parasite attacks (Wcislo 1987; Wcislo and Cane 1996). *Phyocephala* sp., also collected in the emergence-traps, is a parasitoid of bees and is discussed in the next section of this study.

Some natural enemies do not emerge in the same nest aggregation in which they attack their hosts. This can be a problem when the inference about the relationships between natural enemies and hosts is conducted by direct observations. Therefore, the use of emergence-traps allowed us to determine which species of natural enemies actually emerged from the nest aggregation. On the other hand, as in this study we have a mixed species nest aggregation, there were limitations to determine the type of association among some species that emerged in the emergence-traps (see Table 1).

In summary, we suggest that emergence-traps are tools that can aid in studies of solitary bees nesting in the soil. This method allows the measurement of phenology, parasite-host synchrony, parasitism rate, and sex ratio.

### Natural enemies and species associated with the nest aggregation of *E. picta*

Many natural enemies are reported for *Epicharis* species, but there is direct evidence only for *Rhathymus* spp. and *Tetraonyx* spp. (Werneck et al. 2012; Gaglianone et al. 2015; this study). Indirect evidence, however, is reported for species of *Mesoplia* and *Mesonychium* (Apidae, Ericocidini), *Phyocephala* spp. and several species of Mutillidae (Camargo et al. 1975; Hiller and Wittmann 1993; Gaglianone 2005; Rocha-Filho et al. 2008; Luz et al. 2016). Regarding cleptoparasitism on *E. picta*, our data show that there is direct evidence only for *R. friesei*, *T. sexguttata* and *T. aff. lycoides*. *Rhathymus friesei* was the most abundant cleptoparasitic species observed in this study. Even though it is not possible to determine specificity relationships between *Rhathymus* species and *Epicharis* subgenera, there is specificity in the cleptoparasite-host relationship between the genera *Rhathymus* and *Epicharis* (Werneck et al. 2012). On the meloid beetles, there are data on the relationship of *Tetraonyx* spp. to *E. dejeanii* Lepeletier, 1841 (Hiller and Wittmann 1994), *E. nigrita* (Gaglianone 2005; Martins et al. 2019), *E. bicolor* (Rocha-Filho et al. 2008), and *E. picta* (Gaglianone et al. 2015).

*Phyocephala* is a genus composed of parasitoid species that mainly attack adult Hymenoptera. Among neotropical bees, the host records of these Conopidae are for Bombini, Centridini, Euglossini, Megachilini, Tapinotaspidini, and Xylocopini (Rasmussen and Cameron 2004; Melo et al. 2008; Santos et al. 2008; Rocha-Filho and Melo 2011; Stuke et al. 2011; Almada et al. 2020). For *Epicharis*, there are records from indirect evidence that *P. bipunctata* may parasitize *E. bicolor* (Rocha-Filho et al. 2008; Santos et al. 2008). Although data from emergence-traps record *Phyocephala* sp., our evidence is indirect, not corroborating this relationship of parasitism on *E. picta*.

The Mutillidae is composed of parasitic wasps that attack Hymenoptera in general, with records for bees as hosts (Brothers et al. 2000; Luz et al. 2016). Although some studies report the parasite-host relationship between these wasps and *Epicharis*, there is no direct evidence of this relationship (Rocha-Filho et al. 2008). Luz et al. (2016) compiled the data known for host bees of these wasps and these authors consider Apidae to be the main hosts of Mutillidae in the Neotropical region. For *Centris*, nine records of Mutillidae species as parasitoids are known (see Luz et al. 2016), whereas for *Epicharis*, the only record is for *Hoplomutilla myops myops* (Burmeister, 1854), considered as a potential parasitoid of *E. bicolor* (Rocha-Filho et al. 2008). In the present study, it was only possible to observe *Traumatomutilla* sp. approaching the nests of *E. picta*, although it was not seen entering nor leaving the nests.

*Apiomerus* are predators, some species being reported as common predators of bee species, such as stingless bees (Apidae, Meliponini) (Silva and Gil-Santana 2004), and *Apis mellifera* Linnaeus, 1758 (Apidae, Apini) (Silva and Amaral 1973; Amaral-Filho et al. 1994; Marques et al. 2003, 2006). In this study, we show direct evidence that this hemipteran preys on *E. picta*. Until now, no species of *Epicharis* had been associated with this predator. Data on the biology of *A. lanipes* and its mode of predation are still scarce in the literature and it will be necessary to study whether it is a predator specialized in bees.

## Acknowledgements

We would like to thank Fernando A. Silveira and Fernando Mendes for their initial critical reading that contributed to improve this manuscript. We also thank the taxonomists Gabriel Melo (Apidae, Crabronidae and Sphecidae), Danuncia Urban (*Hypanthidium nigritulum*), Juan Tunon and Paschoal Grossi (Meloidae), Roberto Cambra (Mutillidae), Marcel Hermes (Eumeninae), and Paulo Fiúza (*Apiomerus lanipes*). For the photos on Fig. 4, we thank Professor José Lino-Neto (UFV). The authors are grateful for the comments of the anonymous reviewers. The financial support of this study was from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES and Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq.

## References

- Aguiar CML, Gaglianone MC (2003) Nesting biology of *Centris* (*Centris*) *aenea* Lepeletier (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia 20: 601–606. <https://doi.org/10.25085/rsea.790307>
- Almada V, Demarchi L, Ferreras EO, Stuke JH, Clements DK, Lucia M (2020) *Phyocephala inhabilis* (Diptera: Conopidae) as a parasitoid of *Megachile* (*Sayapis*) *bomplandensis* (Hymenoptera: Megachilidae) in Argentina. Revista de la Sociedad Entomológica Argentina 79(3): 45–47.

- Amaral-Filho BF, Góia I, Waib CM, Mendelek E, Cônsoli FL (1994) Observações sobre a biologia de *Apiomerus lanipes* (Fabricius) (Hemiptera, Reduviidae). Revista Brasileira de Zoologia 11: 283–288. <https://doi.org/10.1590/S0101-81751994000200012>
- Batra SWT (1984) Solitary bees. Scientific American 250: 86–93. <https://doi.org/10.1038/scientificamerican0284-120>
- Bossert S, Murray EA, Almeida EAB, Brady SG, Blaimer BB, Danforth BN (2019) Combining transcriptomes and ultraconserved elements to illuminate the phylogeny of Apidae. Molecular Phylogenetics and Evolution 130: 121–131. <https://doi.org/10.1016/j.ympev.2018.10.012>
- Brothers DJ, Tschuch G, Burger F (2000) Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects. Insectes Sociaux 47: 201–211. <https://doi.org/10.1007/PL00001704>
- Camargo JMF, Zucchi R, Sakagami SF (1975) Observations on the bionomics of *Epicharis (Epicharana) rustica flava* (Olivier) including notes on its parasite, *Rhathymus* sp. (Hymenoptera, Apoidea: Anthophoridae). Studia Entomology 18: 313–340.
- Cane JH (1986) Predator deterrence by mandibular gland secretions of bees (Hymenoptera: Apoidea). Journal of Chemical Ecology 12: 1295–1309. <https://doi.org/10.1007/BF01012349>
- Cane JH (1991) Soil of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. Journal of the Kansas Entomological Society 64: 406–413.
- Cope GC, Campbel JW, Grodsky SM, Ellis JD (2019) Evaluation of nest-site selection of ground-nesting bees and wasps (Hymenoptera) using emergence traps. The Canadian Entomologist 151(2): 260–271. <https://doi.org/10.4039/tce.2019.3>
- Costa CCF, Gonçalves RB (2019) What do we know about Neotropical trap-nesting bees? Synopsis about their nest biology and taxonomy. Papéis Avulsos de Zoologia 59: e20195926. <https://doi.org/10.11606/1807-0205/2019.59.26>
- Dec E, Vivallo F (2019) Nesting biology and immature stages of the oil-collecting bee *Epicharis dejeanii* (Apidae: Centridini). Apidologie 50: 606–615. <https://doi.org/10.1007/s13592-019-00673-0>
- Gaglianone MC (2001) Nidificação e forrageamento de *Centris (Ptilotopus) scopipes* Friese (Hymenoptera, Apidae). Revista Brasileira de Zoologia 18(Supl. 1): 107–117. <https://doi.org/10.1590/S0101-81752001000500008>
- Gaglianone MC (2005) Nesting biology, seasonality and flower host of *Epicharis nigrita* (Friese, 1900) (Hymenoptera: Apidae, Centridini), with a comparative analysis for the genus. Studies on Neotropical Fauna and Environment 40: 191–200. <https://doi.org/10.1080/01650520500250145>
- Gaglianone MC, Werneck HA, Campos LAO (2015) Univoltine life cycle of two species of *Epicharis* Klug, 1807 (Apidae, Centridini) and note on tis cleptoparasites *Tetraonyx* spp. (Coleoptera, Meloidae). In: Aguiar AJC, Gonçalves RB, Ramos KS (Eds) Ensaios sobre as abelhas da Região Neotropical: homenagem aos 80 anos de Danuncia Urban. UFPR Press (Curitiba), 397–410.
- Hiller B, Wittmann D (1994) Seasonality, nesting biology and mating behavior of the oil-collecting bee *Epicharis dejeanii* (Anthophoridae, Centridini). Biociências 2: 107–124.

- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Griegger climate classification updated. Meteorologische Zeitschrift 15: 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Laroca S, Reynaud dos Santos DT, Schwartz DL (1993) Observations on the nesting biology of three Brazilian Centridini bees. Tropical Zoology 6: 153–163. <https://doi.org/10.1080/03946975.1993.10539216>
- Laroca S, Nery L (2018) *Epicharis (Epicharoides) decellii*, a new neotropical species of bees (Anthophila, Centridini) from Serra da Mantiqueira region (Penedo, Itatiaia, RJ, Brazil). Acta Biológica Paranaense 47: 1–14. <https://doi.org/10.5380/abpr.v47i0.59869>
- Linsley EG (1958) The ecology of solitary bees. Hilgardia 27: 543–597. <https://doi.org/10.3733/hilg.v27n19p543>
- Litman JR, Praz CJ, Danforth BN, Griswold TL, Cardinal S (2013) Origins, evolution, and diversification of cleptoparasitic lineages in long-tongued bees. Evolution 67: 2982–2998. <https://doi.org/10.1111/evo.12161>
- Luz DR, Waldren GC, Melo GAR (2016) Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae). Revista Brasileira de Entomologia 60: 302–307. <https://doi.org/10.1016/j.rbe.2016.06.001>
- Marques OM, Gil-Santana HR, Magalhães ACA, Carvalho CAL (2003) Predação de *Apiomerus lanipes* (Fabricius, 1803) (Hemiptera: Reduviidae) sobre *Apis mellifera* (Linnaeus, 1758) (Hymenoptera: Apidae), no Estado da Bahia, Brasil. Entomologia y Vectores 10: 419–429.
- Marques OM, Gil-Santana HR, Coutinho ML, Júnior DDS (2006) Percevejos predadores (Hemiptera, Reduviidae, Harpactorinae) em fumo (*Nicotiana tabacum* L.) no município de Cruz das Almas, Bahia. Revista Brasileira de Zoociências 8: 55–59.
- Martins AC, Melo GAR (2016) The New World oil-collecting bees *Centris* and *Epicharis* (Hymenoptera, Apidae): molecular phylogeny and biogeographic history. Zoologica Scripta 45(1): 22–33. <https://doi.org/10.1111/zsc.12133>
- Martins CF, Peixoto MP, Aguiar CML (2014) Plastic nesting behavior of *Centris (Centris) flavifrons* (Hymenoptera: Apidae: Centridini) in an urban area. Apidologie 45: 156–171. <https://doi.org/10.1007/s13592-013-0235-4>
- Martins CF, Neto VIS, Cruz DM (2019) Nesting biology and mating behavior of the solitary bee *Epicharis nigrita* (Apoidea: Centridini). Journal of Apicultural Research 54: 512–521. <https://doi.org/10.1080/00218839.2019.1584963>
- Melo GAR, Faria RR, Marchi P, Carvalho CJB (2008) Small orchid bees are not safe: Parasitismo of two species of *Euglossa* (Hymenoptera: Apidae: Euglossina) by conopid flies (Diptera: Conopidae). Revista Brasileira de Zoologia 25: 573–575. <https://doi.org/10.1590/S0101-81752008000300028>
- Michener CD (1964) Evolution of the nests of bees. American Zoologist 4: 227–239. <https://doi.org/10.1093/icb/4.2.227>
- Michener CD (1974) The Social Behavior of the Bees – A Comparative Study. Cambridge, Balknap, 404 pp.
- Michener CD (2007) The bees of the World. Baltimore: John Hopkins University Press, 953 pp.
- Michener CD, Lange RB (1958) Observations on the Ethology of Neotropical Anthophorine Bees (Hymenoptera: Apoidea). University of Kansas Scienci Bulletin 39: 69–96.

- Morato E, Garcia MVB, Campos LAO (1999) Biologia de *Centris* Fabricius (Hymenoptera, Anthophoridae, Centridini) em matas contínuas na Amazônia Central. Revista Brasileira de Zoologia 16: 1213–1222. <https://doi.org/10.1590/S0101-81751999000400029>
- Moure JS, Urban D, Melo GAR (2007) Catalogue of bees (Hymenoptera: Apoidea) in the Neotropical region. Curitiba: Sociedade Brasileira de Entomologia, [xiv,] 1058 pp.
- Moure JS, Melo GAR, Vivallo F (2012) Centridini Cockerell & Cockerell, 1901. In: Mouré JS, Urban D, Melo GAR (Eds) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region – Online version. <http://moure.cria.org.br/catalogue?id=28982> [Accessed 10 June 2020]
- Parizotto DR (2019) Natural enemies of the oil-collecting bee *Centris analis* (Fabricius, 1804) with notes on the behavior of the cleptoparasite *Coelioxys nigrofimbriata* Cockerell, 1919 (Hymenoptera, Apidae). Journal of Hymenoptera Research 70: 1–16. <https://doi.org/10.3897/jhr.70.33042>
- Radchenko VG (1996) Evolution of the nest building in bees. Entomological Review 75: 20–32.
- Rasmussen C, Cameron SA (2004) Conopid fly (Diptera: Conopidae) attacking large orchid bees (Hymenoptera: Apidae: *Eulaema*). Journal of the Kansas Entomological Society 77: 61–62. <https://doi.org/10.2317/0306.16.1>
- Raw A (1992) Mate searching and populations size of two univoltina, solitary species of the bee genus *Epicharis* (Hymenoptera) in Brazil with records of threats to nesting populations. Entomologist 111: 1–9.
- Rocha-Filho LC, Silva CI, Gaglianone MC, Augusto SC (2008) Nesting behavior and natural enemies of *Epicharis* (*Epicharis*) *bicolor* Smith 1854. (Hymenoptera, Apidae). Tropical Zoology 21: 227–242.
- Rocha-Filho LC, Morato E, Melo GAR (2009) New records of *Aglaomelissa duckei* and a compilation of host association of Ericocidini bees (Hymenoptera: Apidae). Zoologia 26: 299–304. <https://doi.org/10.1590/S1984-46702009000200012>
- Rocha-Filho LC, Melo GAR (2011) Nesting biology and behavioural ecology of the solitary bee *Monoeca haemorrhoidalis* (Smith) and its cleptoparasites *Protosiris gigas* Melo (Hymenoptera: Apidae: Tapinotaspidini; Osirini). Journal of Natural History 45: 2815–2840. <https://doi.org/10.1080/00222933.2011.616271>
- Rocha-Filho LC, Melo GAR (2017) Hide and seek: is the solitary bee *Monoeca haemorrhoidalis* trying to escape from its cleptoparasite *Protosiris gigas* (Hymenoptera, Apidae: Tapinotaspidini; Osirini)? Apidologie 48: 262–270. <https://doi.org/10.1007/s13592-016-0472-4>
- Roubik DW (1989) Ecology and Natural History of Tropical Bees. Cambridge, Cambridge University Press, 514 pp. <https://doi.org/10.1017/CBO9780511574641>
- Roubik DW, Michener CD (1980) The seasonal cycle and nests of *Epicharis zonata*, a bee whose cells are bellow the west-season water table (Hymenoptera, Anthophoridae). Biotropica 12: 56–60. <https://doi.org/10.2307/2387773>
- Rozen JG (1965) The Larvae of the Anthophoridae (Hymenoptera, Apoidea) Part 1. Introduction, Eucerini, and Centridini (Anthophorinae). American Museum Novitates 2233: 1–28.
- Rozen JG (1969) The larvae of the Anthophoridae (Hymenoptera: Apoidea). Part 3. The Melictini, Ericocidini, and Rhathymini. American Museum Novitates 2382: 1–24.

- Rozen JG (1991) Evolution of Cleptoparasitism in Anthophorid Bees as Revealed by Their Mode of Parasitism and First Instars (Hymenoptera: Apoidea). American Museum Novitates 3029: 1–36.
- Rozen JG (2001) A Taxonomic Key to Mature Larvae of Cleptoparasitic Bees (Hymenoptera: Apoidea). American Museum Novitates 3309: 1–27. [https://doi.org/10.1206/0003-0082\(2001\)309%3C0001:ATKTML%3E2.0.CO;2](https://doi.org/10.1206/0003-0082(2001)309%3C0001:ATKTML%3E2.0.CO;2)
- Rozen JG, Buchmann SL (1990) Nesting biology and immature stages of the bees *Centris caesalpiniae*, *C. pallida*, and the cleptoparasitic *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae). American Museum Novitates 2985: 1–30.
- Rozen JG, Melo GAR, Aguiar AJC, Alves-dos-Antos I (2006) Nesting biologies and immature stages of the Tapinotaspidini bee genera *Monoeca* and *Lanthanomelissa* and their Osirine cleptoparasitic *Protosiris* and *Parepeolus* (Hymenoptera: Apidae: Apinae). American Museum Novitates 3501: 1–60. [https://doi.org/10.1206/0003-0082\(2006\)501\[0001:NBAISO\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2006)501[0001:NBAISO]2.0.CO;2)
- Rozen JG, Vinson SB, Coville R, Frankie GW (2011) Biology of the cleptoparasitic bee *Mesoplolia sapphirina* (Ericocidini) and its host *Centris flavofasciata* (Centridini (Apidae: Apinae)). American Museum Novitates 3723: 1–36. <https://doi.org/10.1206/3723.2>
- Rozen JG (2016) Nesting biology of the solitary bee *Epicharis albofasciata* (Apoidea: Apidae: Centridini). American Museum Novitates 3869: 1–8. <https://doi.org/10.1206/3869.1>
- Santos AM, Serrano JC, Couto RM, Rocha LSG, Mello-Patiu CA, Garófalo CA (2008) Conopid flies (Diptera: Conopidae) parasitizing *Centris (Heterocentris) analis* (Fabricius) (Hymenoptera: Apidae, Centridini). Neotropical Entomology 37: 606–608.
- Sardiñas HS, Kremer C (2014) Evaluating nesting microhabitat for ground-nesting bees using emergence traps. Basic and Applied Ecology 15(2): 161–168. <https://doi.org/10.1016/j.baae.2014.02.004>
- Silva AL, Amaral, E (1973) Nota prévia sobre alguns dados bionômicos do predador de abelhas *Apiomerus nigrilobus* Stal, 1872 obtidos em condições de laboratório. Anais da EAV. Universidade Federal de Goiás. n1.
- Silva AC, Gil-Santana HR (2004) Predation of *Apiomerus pilipes* (Fabricius) (Hemiptera, Reduviidae, Harpactorinae, Apiomerini) over Meliponinae bees (Hymenoptera, Apidae), in the State of Amazonas, Brazil. Revista Brasileira de Zoologia 21: 769–774. <https://doi.org/10.1590/S0101-81752004000400007>
- Stuke JH, Lucia M, Abrahamovich AH (2011) Host records of *Physocephala wulpi* Camras, with a description of the puparium (Diptera: Conopidae). Zootaxa 3038: 61–67. <https://doi.org/10.11646/zootaxa.3038.1.6>
- Thiele R, Inouye BD (2007) Nesting Biology, Seasonality, and Mating Behavior of *Epicharis metatarsalis* (Hymenoptera: Apidae) in Northeastern Costa Rica, Annals of the Entomological Society of America 100: 596–602. [https://doi.org/10.1603/0013-8746\(2007\)100\[596:NBSAMB\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2007)100[596:NBSAMB]2.0.CO;2)
- Vélez D, Silveira FA (2006) Synonymic note on *Epicharis (Triepicharis)* Moure 1945 (Hymenoptera: Apidae). Lundiana 7: 151–154.
- Veloso HP, Rangel-Filho AL, Lima JCA (1991) Classificação da vegetação brasileira, adaptada a um sistema universal. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, 124 pp.

- Vesey-FitzGerald D (1939) Observations on bees (Hymenoptera: Apoidea) in Trinidad, B.W.I. Proceedings of the Royal Entomological Society of London 14: 107–110. <https://doi.org/10.1111/j.1365-3032.1939.tb00061.x>
- Vinson SB, Frankie GW (1991) Nest variability in *Centris aethyctera* (Hymenoptera: Anthophoridae) in response to nesting site conditions. Journal of the Kansas Entomological Society 64: 156–162.
- Vivallo F (2020a) Nesting behavior of the oil-collecting bee *Epicharis (Triepicharis) analis Lepeletier* (Hymenoptera: Apidae) in an urban area of Rio de Janeiro, RJ, Brazil. Journal of Apicultural Research 110: e2020025. <https://doi.org/10.1590/1678-4766e2020025>
- Vivallo F (2020b) Nesting biology of the oil-collecting bee *Epicharis (Hoplepicharis) fasciata* (Hymenoptera: Apidae) in an urban area of Rio de Janeiro, RJ, Brazil. Iheringia, Série Zoologia. <https://doi.org/10.1590/1678-4766e2020025>
- Wcislo WT (1987) The roles of seasonality host synchrony and behavior in the evolutions and distributions of nest parasites in Hymenoptera (Insecta). With special reference to bees (Apoidea). Biological Review 63: 515–544. <https://doi.org/10.1111/j.1469-185X.1987.tb01640.x>
- Wcislo WT, Cane JH (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by nnatural enemies. Annual Review of Entomology 41: 257–286. <https://doi.org/10.1146/annurev.en.41.010196.001353>
- Werneck HA, Melo GAR, Campos LAO (2012) First host record for the cleptoparasite bee *Rhathymus friesei* Ducke (Hymenoptera). Revista Brasileira de Entomologia 56: 519–521. <https://doi.org/10.1590/S0085-56262012000400021>
- Werneck HA, Luz CFP, Campos LAO (2015) Tipos polínicos coletados por *Epicharis (Epicharoides) picta* (Smith, 1874) (Apidae: Centridini) em um fragmento de Mata Atlântica. In: Aguiar AJC, Gonçalves RB, Ramos KS (Eds) Ensaios sobre as abelhas da Região Neotropical: homenagem aos 80 anos de Danuncia Urban. 1<sup>st</sup> Edition, UFPR (Curitiba), 295–306.